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Research Article

Butterfly community composition along a vegetation gradient in the Sierra Chiquita, Mexico

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Abstract

This study compares the variation of richness, abundance, and diversity of butterfly species for vegetation communities along an elevational gradient and during different seasons in the Priority Region for Conservation of Biodiversity, Sierra Chiquita, located in the northeast of Mexico. We also analyze the influence of environmental variables on the abundance and richness of butterfly species. Seven sampling sites were established based on criteria of vegetation distribution per altitudinal gradient. Sampling was on a monthly basis and carried out in six permanent plots at each site, using an aerial entomological net during November 2015 to October 2016. A total of 38,011 specimens, representing six families and 195 species, were collected. All parameter values showed significant differences across sites, except between thorn forest and gallery forest. Seasonality effect was absent on richness and diversity species; however, for species abundance, the differences between dry season and rainy season were significantly different in each site except for the comparison of thorn forest and gallery forest. The association between the environmental variables and butterfly communities in the elevational gradient was significant, being the dew point, the solar radiation, the canopy leaf area, and the number of flowering plants the most important variables. The present work represents an important contribution of the vegetation communities variation in richness, abundance, and diversity of butterflies in the northeast of Mexico. These results highlight the importance of the conservation of this heterogeneous habitat and establish reference data for the diurnal Lepidoptera fauna of the region.

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Resumen

En este estudio se compara la variación de la riqueza, abundancia y diversidad de especies de mariposas para comunidades vegetales a lo largo de un gradiente altitudinal y durante diferentes estaciones del año en la Región Prioritaria para la Conservación de la Biodiversidad Sierra Chiquita, ubicada en el noreste de México. Asimismo, se analiza la influencia de las variables ambientales en la abundancia y riqueza de especies de mariposas. Se establecieron siete sitios de muestreo con base en criterios de distribución de la vegetación por gradiente altitudinal. Los muestreos fueron mensuales y se llevaron a cabo en seis parcelas permanentes de cada sitio, utilizando una red entomológica aérea durante noviembre de 2015 a octubre de 2016. Se recolectaron un total de 38,011 especímenes pertenecientes a seis familias y 195 especies. Todos los valores de los parámetros fueron significativamente diferentes entre todos los sitios, excepto para la comparación entre bosque espinoso y bosque de galería. El efecto de la estacionalidad estuvo ausente sobre la riqueza y diversidad de especies; sin embargo, para la abundancia de especies

las diferencias entre la época seca y la época de lluvias fueron significativamente diferentes en cada sitio, excepto para la comparación entre bosque espinoso y bosque de galería. La asociación entre las variables ambientales y las comunidades de mariposas en el gradiente altitudinal fue significativa, siendo el punto de rocío, la radiación solar, el área foliar del dosel y el número de plantas con flores las variables más importantes. El presente trabajo representa una importante contribución de la variación de las comunidades vegetales en la riqueza, abundancia y diversidad de mariposas en el noreste de México. Estos resultados resaltan la importancia de la conservación de este hábitat heterogéneo y establecen datos de referencia para la lepidóptera diurna de la región.

Key words: Community patterns, Papilionoidea, priority land region, seasonality, Tamaulipas, vegetation communities

Introduction

Butterflies belong to the superfamily Papilionoidea, with 18,768 species worldwide (Nieukerken et al. 2011; Llorente et al. 2014), with over 1,900 species in Mexico (Llorente et al. 2014), representing slightly more than 10% of the global diversity. Butterflies are among the best environment quality indicator insects because they are highly diverse and abundant (Prince-Chacón et al. 2011), easy to identify in the field, and due to their rapid biological cycles, they can be sampled throughout the year (Freitas et al. 2006). Additionally, butterflies are significantly impacted by landscape changes as they are closely tied to vegetation (Marín et al. 2014), and most of their life cycle is associated with specific plants (Orozco et al. 2009). Furthermore, they respond to the stratification of the vegetation in terms of light, wind, humidity, and temperature gradients (Montero-Muñoz et al. 2013). Therefore, they are very sensitive to climatic and ecological variations occurring in natural gradients, such as elevation (Camero et al. 2007).

Numerous studies show the close association between altitude and changes in species composition and diversity (Muñoz and Amarillo-Suárez 2010; Pires et al. 2020). Several hypotheses have been proposed to explain these changes. For example, the Rapoport effect states that the richness and distribution ranges of species are inversely related to altitude, with higher richness at low elevations (Sanders 2002). Meanwhile, the hypothesis of mid-domain indicates that the greatest number of species occurs at intermediate altitudes (Brown and Lomolino 1998). Additionally, McCoy (1990) determined that, if the distribution differs between elevations, the time scale used would strongly influence the evaluation of species richness. Thus, seasonal variations are strongly linked to elevational patterns of communities (Castro and Espinosa 2016).

In Mexico, several checklists of butterflies from altitudinal transects ranging from 600 to 3,100 m asl, including different vegetation types, have been published (Llorente et al. 1986; Luis and Llorente 1990; Raguso and Llorente 1990; Luis et al. 1991; Vargas et al. 1994, 1999; Díaz-Batres et al. 2001; Luna and Llorente 2004; Luna et al. 2008; Luna et al. 2010; De la Maza and De la Maza 2015, 2017, 2021; Álvarez et al. 2016). In addition, on a temporal level, the climatic factors influencing butterfly species turnover have been addressed in previous studies (Luis and Llorente 1990, 1993; Vargas et al. 1994; Hernández-Mejía et al. 2008; Luna et al. 2008; Pozo et al. 2008; Luna et al. 2010). However, little is known about the entomofauna and especially about the butterfly ecology of the extreme, humid, and

dry environments of northeastern Mexico, which is inhabited by a very special group that represents about 15% of the national entomofauna and harbors elements of the Atlantic District of the United States (De la Luz and Madero 2011). Knowing the distribution of the species richness and abundance of butterflies in altitudinal gradients allows us to elucidate patterns and processes of biological diversification, which plays an important role in demonstrating the conservation value of a particular habitat (DeVries and Walla 2001). Likewise, the study of communities and populations of butterflies over time can offer important information for implementing urgent measures before the effects of environmental disturbance become irreversible (Núñez-Bustos et al. 2011).

In this context, the Sierra Chiquita, which is an isolated orographic unit within the coastal plain of the North Gulf of Mexico (Treviño et al. 2002), is considered an area of special interest for conservation and requires an evaluation of its natural resources (Arriaga et al. 2000). The objectives of the study were: (1) identify the butterfly species richness in the Sierra Chiquita, northeast Mexico; (2) compare the variation in abundance, richness and diversity of butterfly species along an altitudinal gradient and during the seasons of the year; and (3) analyse the influence of environmental variation (temperature, relative humidity, solar radiation and vegetation cover) on the abundance and richness of butterfly species. Our hypothesis is that the composition and diversity of butterflies decrease with respect to the increase in elevations levels in the Sierra Chiquita.

Methods

Study area

The Sierra Chiquita is located in the central-western portion of the State of Tamaulipas, between 24°23.03' and 24°51.60'N, and 98°32.40' and 99°12.04'W (Fig. 1). Sierra Chiquita (also known as the Sierra de San Carlos or Sierra de Cruillas) is a physiographic discontinuity in the Coastal Plain of the Gulf of Mexico. Due to its relative geographical isolation in relation to the Sierra Madre Oriental, it can be conceived as an ecological island, where relatively particular populations and communities have originated or been conserved (Briones-Villarreal 1991). The area is considered a Mexican Priority Region for Conservation of Biodiversity (RTP) by the National Commission for the Knowledge and Use of Biodiversity (CONABIO). The vegetation types of this RTP mainly include temperate ecosystems in the mountainous areas and various types of scrub vegetation in the piedmont (Arriaga et al. 2000). A main characteristic of the region is that it represents the boreal limit of the cloud forest in northeastern Mexico (Valdez-Tamez et al. 2003). The climate of the region is semi-warm sub-humid with summer rains; the average annual temperature is 18 to 22 °C, and the annual precipitation ranges between 500 and 2,500 mm (Treviño et al. 2002).

Selection of sampling sites

The sampling sites were selected based on Llorente (1984) and Briones-Villarreal (1991) criteria for the elevational gradient and vegetation types. We selected seven sampling sites distributed in four localities within Sierra Chiquita (Fig. 1). The first locality was Cerro El Diente, which included three sampling sites:

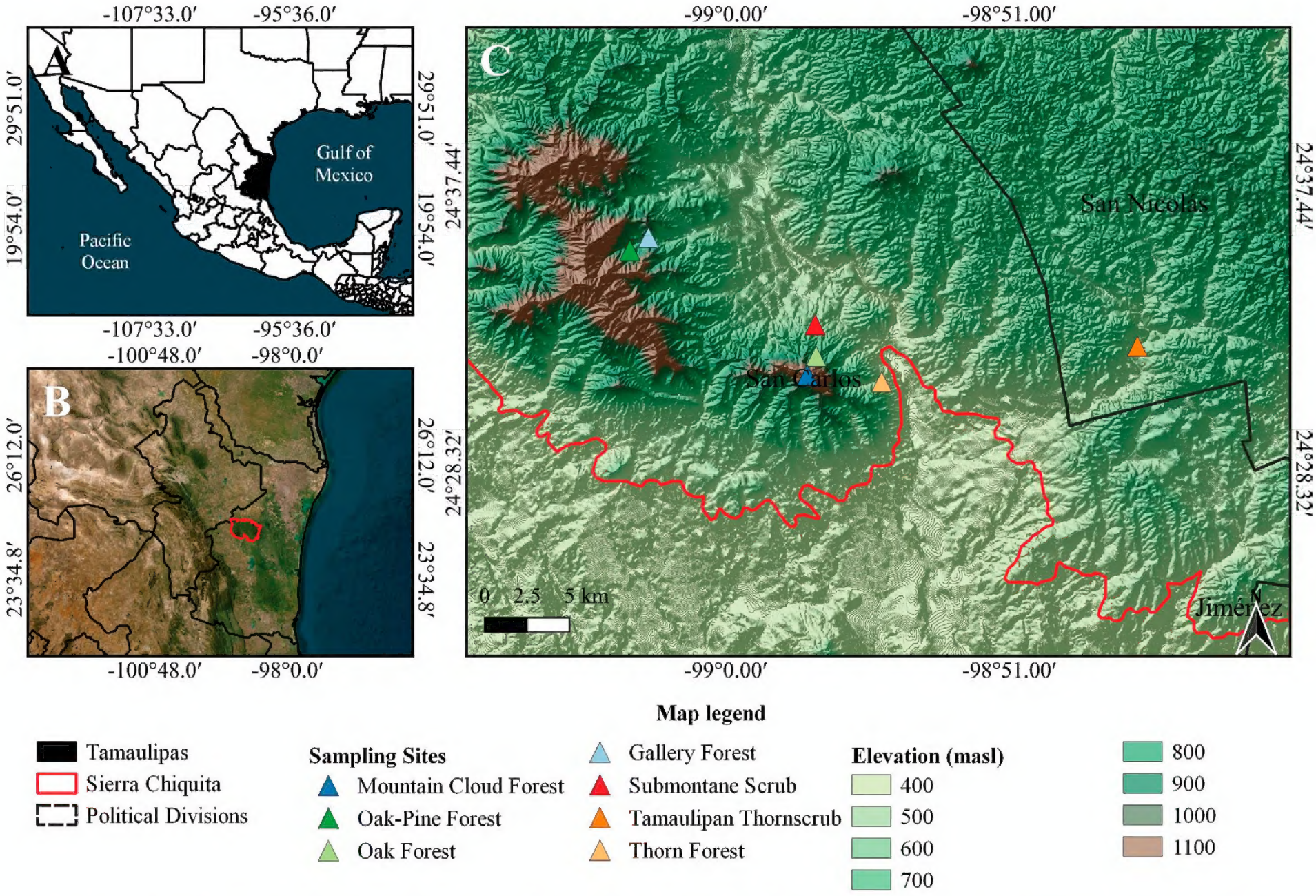

Figure 1. Study area **A** location of Tamaulipas in Mexico **B** location of the Sierra Chiquita within Tamaulipas **C** location of the sampling sites according to the elevation and vegetation type.

Site 1) containing submontane scrub vegetation (SS) (24°33.04'N, 98°57.16'W), at a mean elevation of 550 m asl; Site 2) had oak forest vegetation (OF) (24°32.04'N, 98°57.13'W), at a mean elevation of 960 m asl; and Site 3) with cloud forest vegetation (CF) (24°31.44'N, 98°57.41'W), at a mean elevation of 1080 m asl. The second locality was Carricitos y Tinajas, which had two sampling sites: Site 4) with gallery forest vegetation (GF) (24°35.807'N, 99°2.450'W), at a mean elevation of 730 m asl; and Site 5) containing oak and pine forest vegetation (OPF) (24°35.397'N, 99°3.037'W), at a mean elevation of 820 m asl. The third locality was San Nicolás with a sampling site: Site 6) with Tamaulipan thornscrub vegetation (TTS) (24°32.356'N, 98°46.936'W), at a mean elevation of 500 m asl. The fourth locality was La Encantada with a sampling site: Site 7) with thorn forest vegetation (TF) (24°31.22'N, 98°55.05'W), at a mean elevation of 460 m asl. (Table 1). All localities are located within areas of extreme conservation priority (CONABIO 2007).

During October 2015, the analysis of preliminary samples obtained in the study area was carried out. The Clench model was used to calculate the minimum sample size to be used, based on the method and parameters indicated by Jiménez-Valverde and Hortal (2003). According to the analysis, between 5 and 8 sampling units are needed to register 95% of the richness of each site. Butterflies were assessed using 42 sampling round plots (of radius 10 m), which were evenly distributed among the seven vegetation types (six plots per vegetation type). The plots were previously and randomly located within each of these sites, using GIS software (Suppl. material 1).

Table 1. Descriptive synthesis of the sampling sites.

Vegetation	Elevation	Frequent species	General description
Thorn forest (TF)	460 m asl	*Colubrina elliptica*, *Ebenopsis ebano*, *Phyllostylon brasiliense*, *Randia aculeata*, *Sideroxylon celastrinum*, *Yucca treculeana*, *Zanthoxylum fagara* and *Ziziphus obtusifolia.*	Is a low-strata community, dominated by thorny trees. Most species in this forest are leafless during long periods during the dry season. Only *Ebenopsis ebano*, which is a dominant species, is left without leaves for a very short period.
Tamaulipan thornscrub (TTS)	500 m asl	*Acacia farnesiana*, *Acacia rigidula*, *Castela tortuosa*, *Cercidium macrum*, *Condalia hookeri*, and *Prosopis juliflora.*	Shrub or sub-arboreal community formed by the dominance of thorny species, deciduous for a large part of the year, or aphyllous (leafless).
Submontane scrub (SS)	550 m asl	*Acacia berlandieri*, *Acacia rigidula*, *Cordia boissieri*, *Havardia pallens*, *Helietta parvifolia* and *Leucophyllum frutescens.*	The physiognomy of this community is provided by the upper shrub layer, whose height varies between 2.5 and 5.0 m and reaches coverage of up to 70%. It is characterized by *Helietta parvifolia*, an unarmed rutaceae that gives the vegetation a uniform structure, as it is normally the only dominant one.
Gallery forest (GF)	730 m asl	*Fraxinus greggii*, *Platanus occidentalis*, *Populus mexicana*, and *Salix humboldtiana.*	Tree community that develops on the banks of rivers and streams, always under humid conditions.
Oak forest (OF)	960 m asl	*Arbutus xalapensis*, *Quercus canbyi*, *Quercus clivicola*, and *Quercus virginiana.*	These communities are made up of different species of oaks of the Quercus genus. These forests are generally found as a transition between coniferous forests and jungles.
Oak and pine forest (OPF)	820 m asl	*Arbutus xalapensis*, *Carya ovata*, *Persea podadenia*, *Pinus pseudostrobus*, *Platanus occidentalis*, *Prunus serotina*, *Quercus laceyi*, and *Quercus rysophylla.*	These communities are made up of oaks and, to a somewhat lesser extent, pines. They are evergreen and deciduous trees; flowering and fruiting are variable throughout the year.
Cloud forest (CF)	1080 m asl	*Abies guatemalensis*, *Acer saccharum*, *Carpinus caroliniana*, *Carya ovata*, *Crataegus rosei*, *Ilex rubra*, *Liquidambar styraciflua*, and *Ostrya virginiana.*	Physiognomically, it is a dense forest that develops in regions of rugged relief and steep slopes; it is common to find it in ravines protected from winds and strong sunshine.

Sampling and processing of specimens

Within each plot, we recorded the frequencies of all adult butterflies over a period of 20 minutes. Butterfly sampling was conducted monthly (from November 2015 to October 2016) in each of the plots and in all vegetation types in order to record all possible species. During the sampling, we had permission from the local authorities. We collected butterflies directly using entomological nets following the techniques recommended by Villarreal et al. (2006).

A representative percentage of the collected specimens was mounted according to the described procedure of Andrade et al. (2013). For taxonomic identification of specimens at the species level, the works of Scott (1986), Llorente et al. (1997), Luis et al. (2003), Garwood and Lehman (2005), Vargas et al. (2008), Luis et al. (2010), Glassberg (2018), and De la Maza and De la Maza (2019, 2022) were consulted. For the reclassification of species to subspecies, the interactive list and the phylogenetic ordering of Warren et al. (2024) were taken as references. All the specimens were labeled and deposited in the entomological collection of the Engineering and Sciences Faculty at the Autonomous University of Tamaulipas, Victoria, Tamaulipas, Mexico.

Organization of seasonal data

The seasons were defined based on the historical data of the monthly total values of temperature and rainfall (average from 2005 to 2014), which were obtained from MODIS images obtained from the GIOVANNI online server and plotted to visually analyze the fluctuation of these parameters. On this basis, two seasons were defined: the dry season (November to April) and the rainy season (May to October) (Fig. 2).

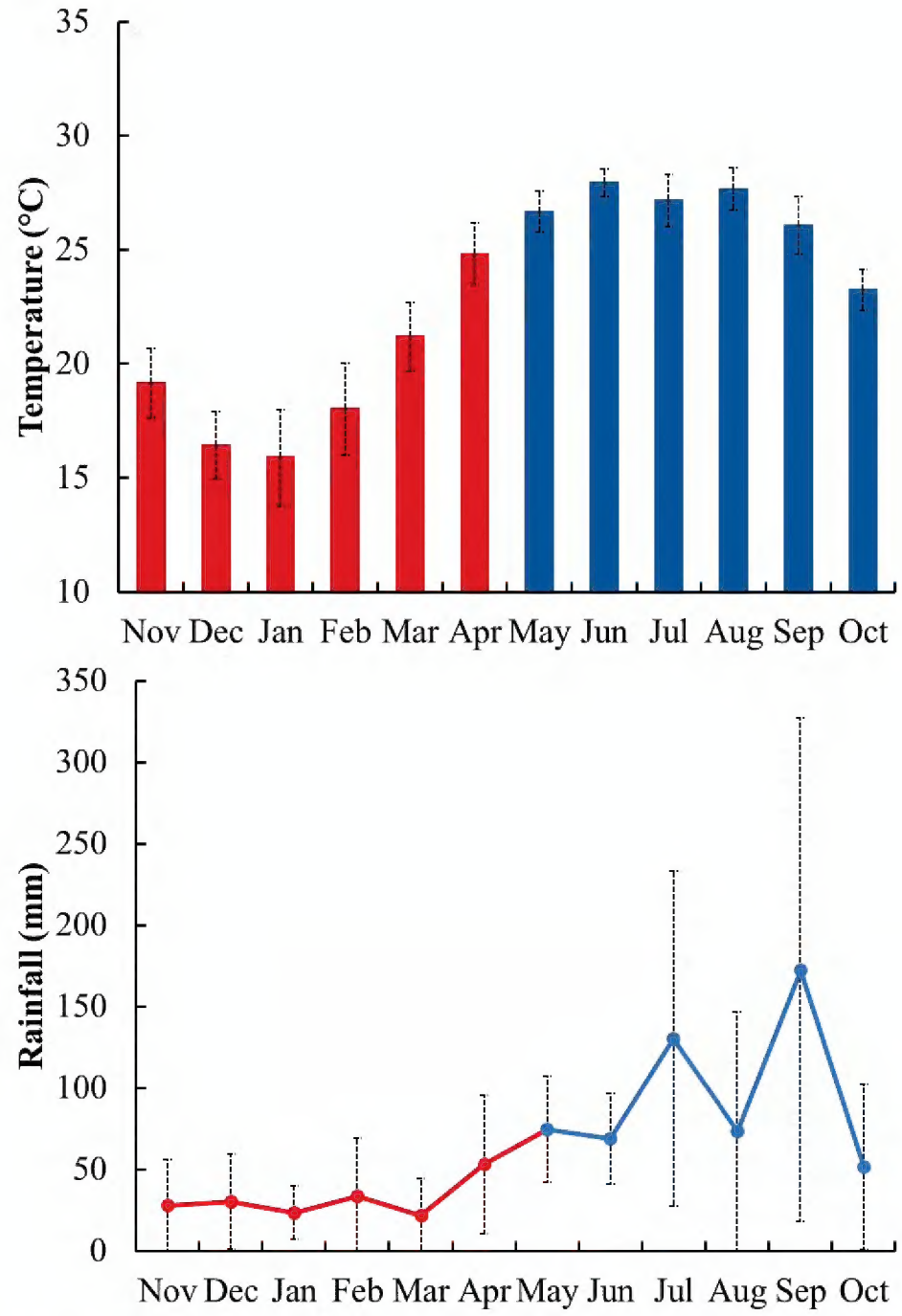

Figure 2. Monthly average variation of temperature and rainfall in the Sierra Chiquita. Dry season (red color) and rainy season (blue color).

Microenvironment measurement

The microenvironmental variables were measured in each plot using a Kestrel 3500 portable weather station, a LX-101A digital luxmeter, and a convex spherical densiometer, simultaneously with the sampling of the butterflies, recording the following variables: maximum wind speed (MWS) and average wind speed (AWS) (obtained during five minutes of exposure), temperature (T), relative humidity (RH), heat index (HI), dew point (DP), evapotranspiration (E), solar radiation (SR), canopy leaf area (CLA), and the number of flowering plants (FP) present during the sampling.

Data analysis

Species richness was measured as the total number of species observed in the study area as well as in each of the sites. Significant differences in the number of species between sites were determined using one-way ANOVA tests in the Statistica 13.3 program (TIBCO Software Inc. 2017). Sampling efficiency was calculated for the entire study area and for each site using the interpolation and extrapolation methodology proposed by Chao and Jost (2012), available in the iNEXT package (Hsieh et al. 2016) for version 3.5.3 of R (R Development Core Team 2019).

Abundance differences between sites were calculated with a one-way ANOVA test. For the analysis of alpha diversity, we adopted the index of Simpson and the analytical method of Chao and Jost (2015) to obtain profiles in which diversity is evaluated in terms of "effective numbers of species" (qD), an approach that is equivalent to the numbers of Hill (Hill 1973). Hill numbers include three widely used measures: species richness (q = 0), Shannon diversity (exponential of Shannon entropy, q = 1), and Simpson diversity (inverse of Simpson concentration, q = 2), all of which are expressed in units of "species equivalents." The analysis was performed for the entire study area and for each site using the SpadeR package (Chao et al. 2016) in R 3.5.3. To examine differences in species composition between sites, we performed non-metric multidimensional scaling (NMDS) analysis, using the Bray-Curtis index as the similarity matrix. A PERMANOVA was also performed to test for differences in species composition between sites. Both analyses were performed using the Vegan package (Oksanen et al. 2019) in R 3.5.3.

The seasonal effect was measured separately, comparing the species richness, abundance, and diversity observed per study site during the dry season (November 2015 to April 2016) and rainy season (May to October 2016). The indexes and statistical tests mentioned above were used for such comparisons: one-way ANOVA tests for differences in species richness and abundance, estimation of species richness, and alpha diversity index, which were performed in Statistica 13.3 and R 3.5.3. In addition, two-way PERMANOVA and NMDS analyses were carried out to include the seasonal effect in the species composition, with the aim of grouping sites and seasons. These analyses were performed in R 3.5.3.

Finally, a canonical correspondence analysis (CCA) was carried out to determine the relationship between the microenvironmental variables and the abundance of the recorded species in each plot, which also includes a Monte Carlo permutation test to evaluate the significance of both the microenvironmental variables as well as the species in the analysis. For the CCA, the average values of the microenvironmental variables of each season of the year were used (dry and rainy season). The CCA was done using the Vegan package in R 3.5.3.

Results

Variation of butterflies per plant community in Sierra Chiquita

A total of 38,011 Papilionoidea specimens were collected, distributed across six families, 20 subfamilies, 38 tribes, 129 genera, and 195 species. Nymphalidae was the most abundant family, with 15,658 individuals, which represents 41% of the total abundance in the study area. A lower abundance was recorded in Hesperiidae (24%), Pieridae (15%), Lycaenidae (11%), Papilionidae (6%) and Riodinidae (3%). The highest species richness was found in the Nymphalidae family with 33% of the total obtained species, followed by Hesperiidae (29%), Lycaenidae (15%), Pieridae (12%), Papilionidae (6%) and Riodinidae (5%) (Suppl. material 2). The sample coverage estimator indicated that our inventory for the Sierra Chiquita is 99.8% complete. Total diversity values of Papilionoidea in the study area were 0.98 for the Simpson index, and using the method of Chao and Jost (2015), there were 195 species for ${}^{0}D$, 162 for ${}^{1}D$, and 145 for ${}^{2}D$.

Both abundance and species richness were significantly different ($p < 0.05$) between all sites, except for the comparison between the sites with TF and GF vegetation (Fig. 3A, B). Both parameters (abundance and species richness) decreased with changes in vegetation with increasing altitudinal gradient. In the site with TF vegetation, 6,011 individuals and 133 species were registered, representing a sampling coverage of 99.8%. In the site with TTS vegetation, the values were reduced to 5,616 individuals and 124 species (coverage of 99.8%). For the site with SS vegetation, the values were increased to 6,362 individuals and 140 species (coverage of 99.8%), to subsequently decrease in the site with GF vegetation with 5,887 individuals and 129 species (coverage of 99.8%), while for OF vegetation, 5,316 individuals and 118 species (coverage of 99.8%) were registered. OPF vegetation registered 4,679 individuals and 102 species (coverage of 99.4%), and CF vegetation registered 4,140 individuals and 88 species (coverage of 99.4%).

Simpson diversity decreased with changes in vegetation with increasing altitudinal gradient and were significantly different ($p < 0.05$) between all sites, except for the comparison between the sites with TF and GF vegetation (Fig. 3C). For ^0D, ^1D, and ^2D, the site with SS vegetation had the highest diversity. All comparisons between sites were significantly different (with 95% confidence intervals), except for the comparison between the sites with TF and GF vegetation (Fig. 4A–C). The one-way PERMANOVA test detected significant differences in species composition between all sites ($SS_{total} = 2.05$; $SS_{within\text{-}group} = 0.25$; $F = 42.15$, $p < 0.001$), except for the comparison between the sites with TF and GF vegetation. Butterfly communities sampled formed separate groups in the NMDS diagram, except for the sites with TF and GF vegetation (Stress = 0.06) (Fig. 5A).

Effect of seasonality on butterfly changes per plant community

In the Sierra Chiquita, the highest abundance and species richness were registered during the rainy season. Both seasons recorded 99.8% inventory completeness.

The differences in the abundance of the dry and rainy seasons were significant ($p < 0.05$) in each site except for the sites with TF and GF vegetation (Fig. 3E). Regarding diversity, the seasonal effect was absent and did not show significant differences between seasons (Fig. 4D–F).

Two-way PERMANOVA allowed us to identify a significant effect of season ($F = 9.287$, $df = 1$, $p < 0.001$) and plant communities (site) ($F = 45.91$, $df = 6$, $p < 0.001$) on species composition. But the interaction between seasons and plant communities was not significant. Butterflies sampled formed separate groups by plant communities in the NMDS ordination diagram (Stress = 0.1) (Fig. 5B).

Butterfly responses to environmental variation

The HI, DP, SR, CLA, and FP were the significant environmental variables ($p < 0.05$) used in the CCA (Table 2). CCA showed significant association between the environmental variables and the butterfly communities with changes in vegetation with increasing altitudinal gradient (total inertia = 96%; $p < 0.05$). The variables most related to the butterfly abundance in the gradient were: SR, CLA, and FP for Axis 1 (eigenvalue = 0.125; inertia = 81.6%). For Axis 2

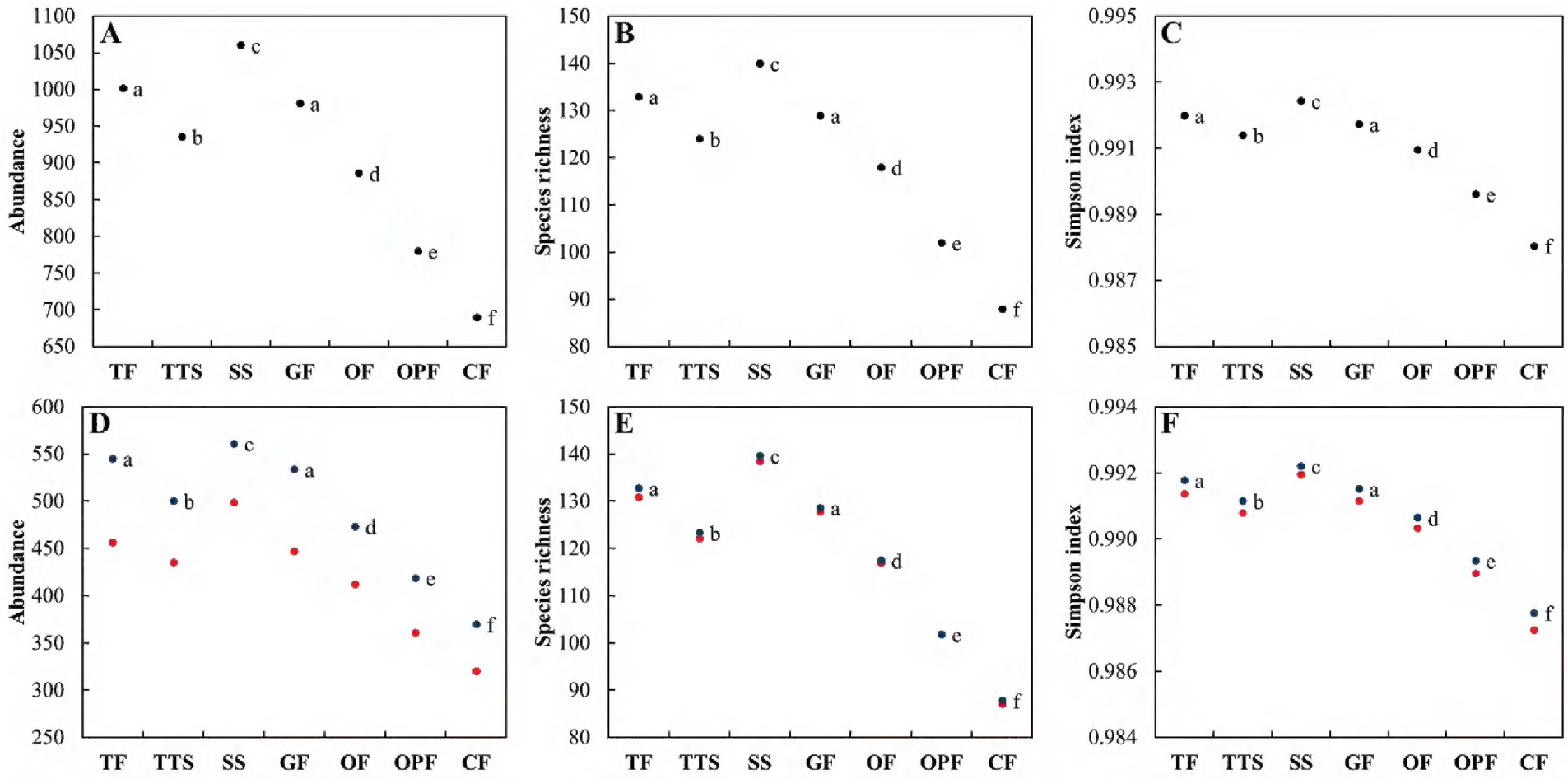

Figure 3. Abundance, species richness, and Simpson diversity for vegetation community and seasons of the year (mean ± standard errors) in the Sierra Chiquita. Different letters represent significant differences between communities ($p < 0.05$). Dry season (red color) and rainy season (blue color).

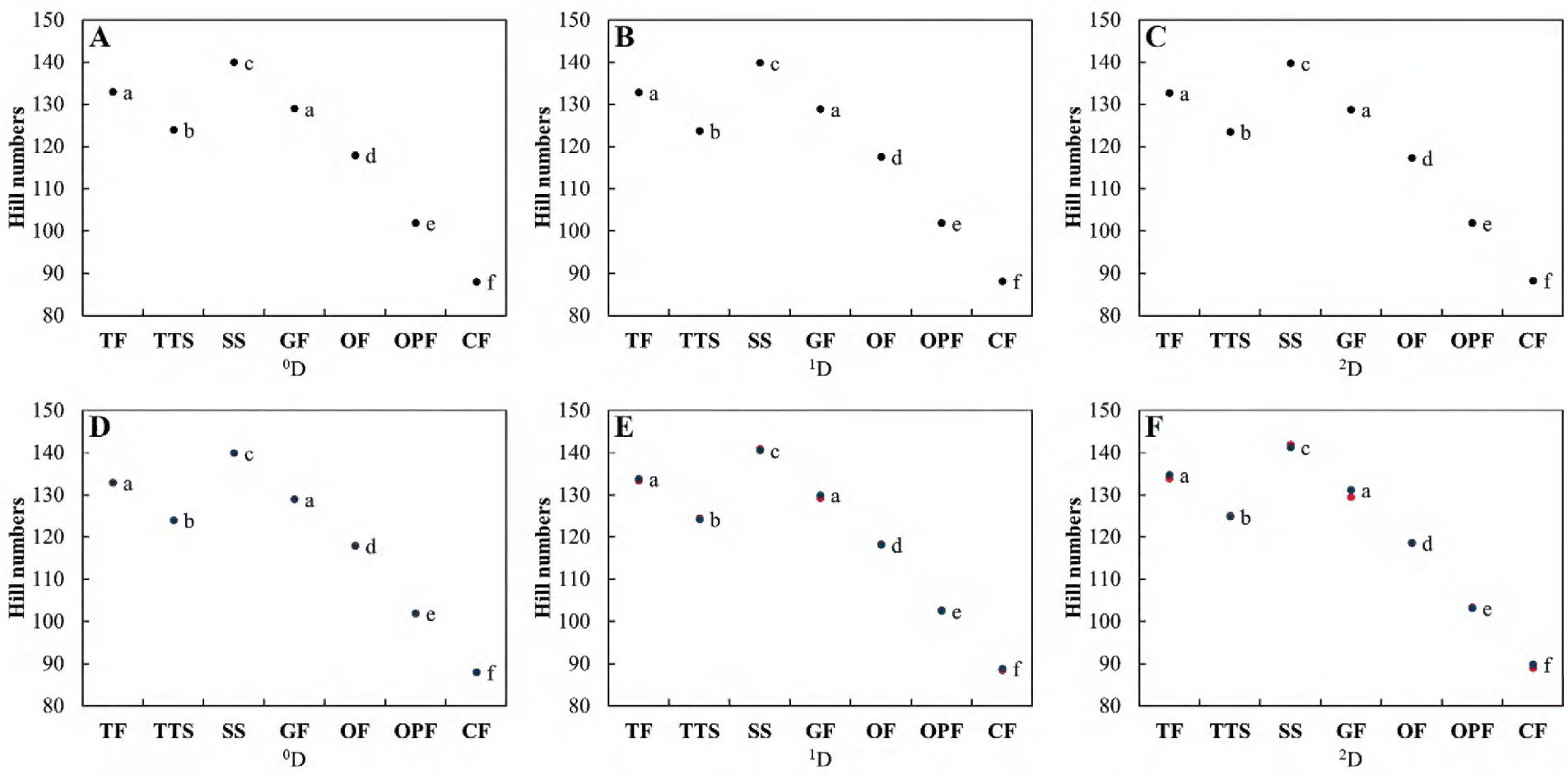

Figure 4. Alpha diversity profiles (^0D, ^1D, and ^2D) for vegetation community and seasons of the year in the Sierra Chiquita. The error bars represent 95% confidence intervals. Dry season (red color) and rainy season (blue color).

(eigenvalue = 0.022; inertia = 14.4%), HI and DP were the most important variables. *Heraclides anchisiades idaeus* (Fabricius, 1793), *Calephelis perditalis perditalis* W. Barnes & McDunnough, 1918, *Asterocampa idyja argus* (H. Bates, 1864), *Dynamine dyonis* Geyer, 1837, *Marpesia petreus* (Cramer, 1776), Chlosyne pardelina Grishin, 2023, *Anthanassa texana* (W. H. Edwards, 1863), *Spicauda procne* (Plötz, 1881), *Pholisora catullus* (Fabricius, 1793), *Burnsius philetas* (W. H. Edwards, 1881) and *Atalopedes huron* (W. H. Edwards, 1863) are associated with conditions of high SR, CLA, and FP, and high HI and DP, environmental

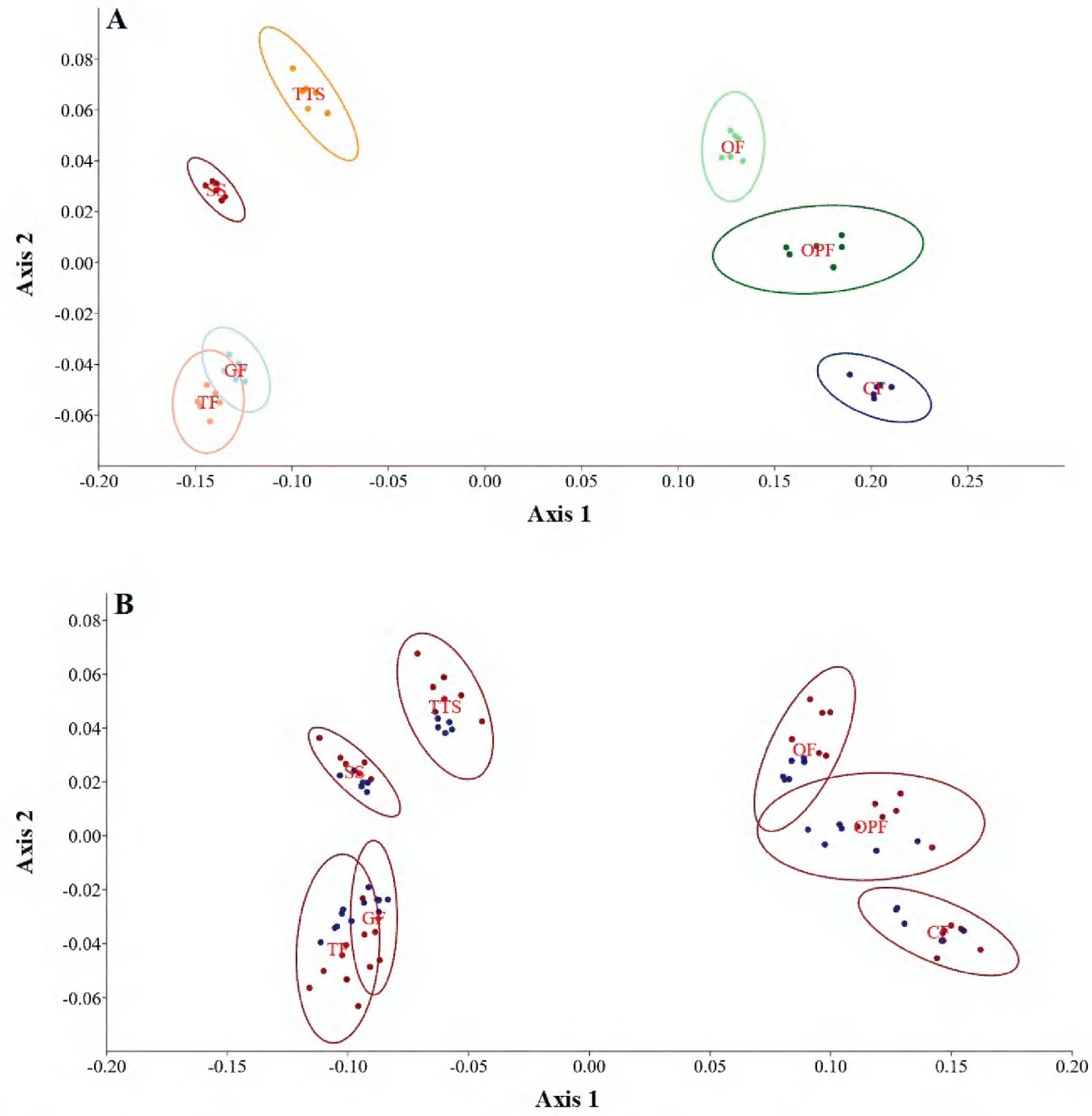

Figure 5. Non-metric multidimensional scaling (NMDS) ordination of the butterfly communities for vegetation community and seasons of the year in the Sierra Chiquita.

Table 2. Environmental values registered for vegetation community in the Sierra Chiquita. Environmental variables marked (*) are significant ($p < 0.05$) according to the Monte Carlo permutation test. MWS = maximum wind speed; AWS = average wind speed; T = temperature; RH = relative humidity; HI = heat index; DP = dew point; E = evapotranspiration; SR = solar radiation; CLA = canopy leaf area; FP = number of flowering plants.

Environment variable	TF	TTS	SS	GF	OF	OPF	CF
MWS (Km/h)	18.1 ± 2.2	19.8 ± 1.5	21.7 ± 2.7	18.9 ± 1.3	19.7 ± 1.9	20.2 ± 2.1	19.9 ± 3
AWS (Km/h)	15.5 ± 2.3	17.1 ± 1.5	19.4 ± 2.3	16.5 ± 1.7	17 ± 1.8	17.7 ± 1.9	17.3 ± 3.1
T (°C)	23.7 ± 1	24.7 ± 2	24.3 ± 1.6	23.7 ± 1.3	23.9 ± 1.8	23.3 ± 1.2	22.9 ± 1.7
RH (%)	64.3 ± 2	68.5 ± 1.5	66.8 ± 3.2	67.1 ± 4.7	65.6 ± 1.8	66.8 ± 4.4	66.5 ± 3.2
HI (°C) *	24.7 ± 1.3	25.6 ± 1.7	25.3 ± 1.4	24.8 ± 1.1	24.9 ± 1.9	24.3 ± 1.1	23.9 ± 1.6
DP (°C) *	16.1 ± 1.3	17.2 ± 1.5	17.4 ± 2.2	16.3 ± 1.5	16.6 ± 2.3	15.7 ± 1.9	15.5 ± 1.8
E (°C)	17.1 ± 1.4	18 ± 1.6	18.5 ± 2.1	17.2 ± 1.7	17.6 ± 2.4	16.9 ± 1.6	16.4 ± 1.9
SR (Klux) *	39.6 ± 5.4	39.5 ± 3.9	39.4 ± 2.4	37.4 ± 3.1	36.1 ± 2	37.9 ± 3.3	35.9 ± 2.2
CLA (%) *	83.7 ± 2.1	83.5 ± 4	82.6 ± 4.8	83.1 ± 3.2	82 ± 2	80.9 ± 3.4	80.7 ± 3.2
FP *	33 ± 5	30 ± 7	34 ± 9	34 ± 8	25 ± 7	29 ± 10	26 ± 4

conditions related to TF and GF vegetation. On the other hand, *Nathalis iole iole* Boisduval, 1836, *Colias eurytheme* Boisduval, 1852, *Anteos clorinde* (Godart, [1824]), *Arawacus jada* (Hewitson, 1867), *Chlorostrymon simaethis sarita* (Skinner, 1895), *Doxocopa druryi acca* (C. Felder & R. Felder, 1867), *Eunica monima* (Stoll, 1782), *Chlosyne bollii* (W. H. Edwards, [1878]), and *Celotes nessus*

(W. H. Edwards, 1877) are related to low SR, CLA, and FP, and high HI and DP, environmental conditions associated to TTS and SS vegetation. Finally, *Pterourus pilumnus* (Boisduval, 1836), *Pterourus alexiares garcia* (Rothschild & Jordan, 1906), *Eurema daira eugenia* (Wallengren, 1860), *Calycopis isobeon* (A. Butler & H. Druce, 1872), *Zizula cyna* (W. H. Edwards, 1881), *Vanessa virginiensis* (Drury, 1773), *Polygonia interrogationis* (Fabricius, 1798), *Anthanassa tulcis* (H. Bates, 1864), and *Telegonus cellus* (Boisduval & Le Conte, [1837]) are related to low SR, CLA, and FP, and low HI and DP, environmental conditions associated to OF, OPF, and CF vegetation (Fig. 6).

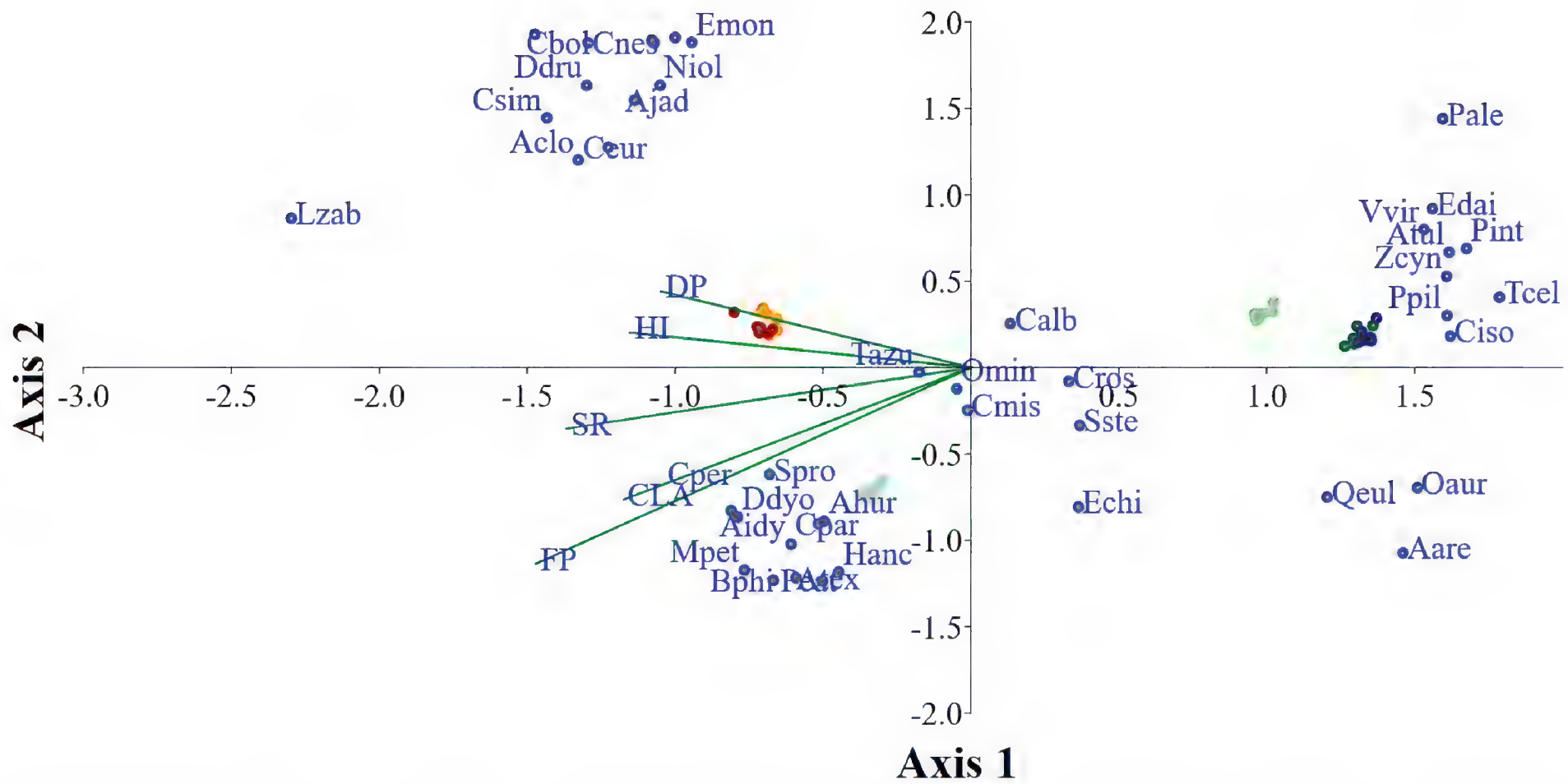

Figure 6. Canonical Correspondence Analysis (CCA) of the butterfly communities and significant environmental variables corresponding to the plant communities sampled. HI = heat index; DP = dew point; SR = solar radiation; CLA = canopy leaf area; FP = number of flowering plants. The meaning of the abbreviations for each species is presented in Suppl. material 2.

Discussion

Butterfly biodiversity in the Sierra Chiquita

In Sierra Chiquita, the superfamily Papilionoidea consists of 195 species that represent 40% of the richness recorded for Tamaulipas (Meléndez-Jaramillo et al. 2024) and 9.5% in relation to Mexico (Warren 2000; Llorente et al. 2006). Nymphalidae are the family with the greatest richness, which represents 44% of the diversity of the family for the state, and 11.8% in comparison with that of the country. The abundance and species richness of families found in this study are very different when compared to some research conducted in other parts of the country. This is due to the specific biotic and abiotic characteristics of each ecoregion, which allow the development of a particular type of fauna (Espinosa et al. 2008), in this case, butterflies. This also may be occurring at the species level, where the characteristics of the area, as well as the presence and abundance of its host plants, will determine the dominant species (Luis and Llorente 1990; Vargas et al. 1994).

When comparing results found in this research with some of the systematic and rigorously sampled inventories of Papilionoidea in Mexico, it can be observed that the species richness in the present study area is high. Luna et al. (2010) recorded 145 species for the Lobos Canyon, Yautepec, Morelos State. In the same way, Luna et al. (2008) recorded 142 species for the Huautla mountain range in the states of Morelos and Puebla. Hernández-Mejía et al. (2008) listed 213 species for Malinalco, State of Mexico. Luna and Llorente (2004) listed 85 species for the four entities that comprise the Sierra Nevada. Bizuet-Flores et al. (2001) obtained 69 species for El Chico National Park, Hidalgo State. Luis and Llorente (1993) listed 161 species for Omiltemi Park, Guerrero. Balcázar (1993) presented 205 species for Pedernales, Michoacán. Luis and Llorente (1990) recorded 65 species for the Dinamos, Magdalena Contreras, D.F. Beutelspacher (1982) listed 141 species for El Chorreadero, Chiapas. This comparison is speculative, as each of these studies has been conducted with very different methodologies and approaches than this research. However, it can be suggested that Sierra Chiquita is a very important area for the distribution and diversity of Papilionoidea in Tamaulipas and Mexico.

Although Van Someren Rydon traps were not used as instruments to increase sampling efficiency in this study, richness estimators suggest that the butterfly fauna was obtained almost entirely in Sierra Chiquita; however, the possibility exists that some species may remain unregistered. In this regard, several authors point out that the increase in number of samples and time of study, or selection of other sampling methods, can aid in complementing faunistic inventories (Sackmann 2006; Hernández-Mejía et al. 2008; Bonebrake and Sorto 2009; Pedraza et al. 2010; Álvarez-García et al. 2016; González-Valdivia et al. 2016). However, the critical value in which a faunal inventory can be considered reliable or complete is from 70% representativeness, since above that limit, the number of samples required to register all the species increases remarkably and disproportionately (Jiménez-Valverde and Hortal 2003). Considering the high percentage of representativeness obtained in this study, it would be necessary to conduct many additional samples only to record a minimum number of possible missing species, since these are considered accidental species that come from adjacent sites (Pozo et al. 2005; Hortal et al. 2006).

Comparing the number of species between different habitats is often enough to give a rapid assessment of a biodiversity measure. However, it is necessary to resort to the use of other statistical measures to make comparisons with other studies (Magurran 2004). In this investigation, quantification of diversity was done mainly by the values obtained from Simpson (0.98). The diversity index of Simpson gives greater weight to the abundant species and underestimates rare ones, returning values between 0 (low diversity) and a maximum of 1- 1/ S (Moreno 2001). This suggests that the diversity of butterflies in the study area is actually very high. Moreover, observed values were higher than the diversity present in some tropical communities, where the existing conditions favor a high number of species and individuals, as observed in Montero-Muñoz et al. (2013) for Tablazo Paramo, Cundinamarca, and Camero et al. (2007) in Combeima River, department of Tolima, both in Colombia.

Elevation effects on diversity patterns of butterflies

Altitude is a variable frequently related to changes in species richness and abundance (Janzen 1973), producing changes in distribution patterns along altitudinal gradients (Llorente 1984; Andrade-Correa 2002), which was demonstrated in this study. In general, a negative correlation of altitude was observed with abundance or species richness—that is, a reduction in the number of specimens and species as the altitudinal gradient increased. According to Andrade-Correa (2002), it is observed that diversity and percentage of exclusive species decrease towards higher altitude areas. Moreover, Hernández-Mejía et al. (2008) state that the overall tendency of richness and abundance is to decrease with the altitudinal gradient. Although each family shows a different rate of decline, Nymphalidae decreases faster, which may be because their higher number of species accentuates the altitudinal effect. Contrarily, the Pieridae family comprises many eurioic species, and therefore the change in richness is almost imperceptible as the altitude increases. In relation to the general abundance of each family, it can be observed how this decreased notably with the increase in altitude. This pattern in the number of individuals has been observed in other studies with butterflies (Luis and Llorente 1990; Vargas et al. 1994, 1999; Andrade-Correa 2002; Luna and Llorente 2004; Palacios and Constantino 2006; Camero et al. 2007; Hernández-Mejía et al. 2008; Ospina et al. 2010; Carrero et al. 2013), as well as in different groups of insects, such as the necrophilous entomofauna (Sánchez-Ramos et al. 1993) and Scarabaeoidea beetles (Morón 1994).

The variation found in community patterns could have its origin in abiotic factors that modify along the altitudinal gradient, such as solar radiation and precipitation, as well as the increase of unfavorable environments and the reduction in availability of resources (McCain and Grytnes 2010). In addition, the available area that species can occupy decreases with altitude, which can lead to a reduction in the number of individuals per species at higher sites, as was observed in the OF, OPF, and CF sites (Camero 2003; Camero et al. 2007). Furthermore, the linear decrease in temperature, which decreases on average 0.68 °C per 100 meters of increase in elevation, is perhaps one of the most important abiotic factors in the altitudinal distribution of species (McCain and Grytnes 2010). Therefore, the lower abundance in the higher altitude sites could be related to their lower temperature, which represents an unfavorable factor for these insects (Kremen et al. 1993; Fagua 1999). The importance of this variable has also been observed in other studies of Lepidoptera (Luis and Llorente 1990; Vargas et al. 1994, 1999; Luna and Llorente 2004; Hernández-Mejía et al. 2008).

According to the behavior of the ecological parameters, abundance, species richness, and diversity in the different sites, it can be suggested that vegetation and perhaps temperature and humidity are the determining factors in the composition of butterfly species in the study area, parameters that decrease with altitude. Protecting populations of Papilionoidea in mountain areas often depends on the conservation of lower adjacent areas, where the greatest abundance may occur (Andrade-Correa 2002). Another issue directly associated with the conservation of the populations is that middle and high mountain areas are frequently used as natural corridors in the migration of butterfly species (Monteagudo-Sabaté et al. 2001). It is also necessary to consider the displacements that occur

from the lower parts towards the higher elevation areas because species search for foraging sites and better climatic conditions (Bonebrake et al. 2010). Therefore, biodiversity inventories along an altitudinal gradient, such as the one carried out in this research, serve as monitoring studies of habitat quality, which allow for identifying important areas in conservation and management policies (Dewenter and Tscharntke 2000; Hoyle and Harborne 2005; Fattorini 2006).

Seasonal effects on diversity patterns of butterflies

Seasonality is a very important factor in species distribution, being of great relevance for insects since they cannot regulate their body temperature and therefore require favorable environmental conditions to perform their metabolic activities and development of their life cycles (Brown 1984; Morón and Terrón 1984; Wolda 1988). Among the microclimatic factors that influence the seasonal distribution of butterflies in the Sierra Chiquita are temperature and relative humidity. This temporal association is commonly recorded in tropical areas (Arteaga 1991; Luis et al. 1991; Vargas et al. 1994, 1999; Balcázar 1993), in which the imagos are most active during the wet seasons, that is, when the availability of resources is greater, wintering in diapause (Scott 1979; Courtney 1986).

Additionally, butterflies are closely associated with plants, and their presence depends on the flora and structure of the vegetation (Shapiro 1974). Thus, it is possible that the wetter conditions in May to October favored the increase of diversity and biomass of the plant community, which can lead to the establishment of more species and larger populations of butterflies (Rhoades 1983). Temperature is more stable in this period, but humidity conditions are contrasting and remarkably superior compared to the dry season, in which the total precipitation is 190 mm, while that in the rainy season is 570 mm. Although the first rains take place in May, the greater precipitation occurs from August to October, and consequently there is greater cloudiness that reduces evaporation. During this season, vegetation diversity and density increase, thus providing a greater number of resources that are used by butterflies for their feeding, oviposition, and protection, which favor the presence of more species with larger populations. Moreover, the presence of rainfall correlates directly with abundance and richness of insects (Wolda 1988), since it affects the physiology of reproduction, the ontogenetic development, and the behavior of the imagoes; indirectly, it can also affect populations because of its effects on plant phenology (Vargas et al. 1999). As in other studies, the rainy season would represent the period when the greatest number of Lepidoptera species complete their diapause stage and begin their feeding, reproduction, and oviposition stage (Owen 1971; Wolda 1988).

On the contrary, the highest variation in temperature as well as the highest number of clear days occur during the months of November to April, leading to high evaporation rates. Under these conditions, most of the vegetation is dry, especially some herbaceous plants that, when flowering, provide food for imagoes. During the drought period, water reserves of tree and shrub species are also reduced, modifying their growth, nectar production, nutritional content, or even texture and turgor of leaves, which constitute food resources for most lepidoptera species. Therefore, although trees and shrubs are present in the habitat, many of them cannot be used by butterflies during this period due to their deciduous phenology, affecting in this way the community composition and

populations of butterflies in these months. In addition, some compounds present in plants can vary in each season and not be palatable in certain months, so they are not nutritious for the immature stages of many species. Nevertheless, it is possible that the species is in diapause during the cold months (Scott 1979).

Butterflies responses to environmental variation

Some studies on butterfly ecology have sought to analyze the variables that determine the faunal composition of the communities of this group, including host plants (Scoble 1992; Hall and Willmott 2000; DeVries and Walla 2001; O'Brien et al. 2003; Boggs and Dau 2004), some of the factors related to diapause, migration, and seasonality (Scott 1979; Janzen 1987; Jones and Rienks 1987), temporal fluctuation (Vasconcellos-Neto 1991; Freitas 1996; Freitas et al. 2001), spatial structure (Brown 1981; Mallet 1986), predation (Janzen 1988; Chai and Srygley 1990; Lyytinen et al. 2004), and competition (Benson 1978). However, in most previous studies, the analysis was carried out on a community basis. On that basis, this research constitutes one of the first studies where the response is analyzed independently for each of the species. The CCA used here constitutes a recent method (Oksanen et al. 2019) and therefore has been used in few studies; for example, to explain how variables influence the floristic composition along an urbanization gradient (Meléndez-Jaramillo et al. 2023).

The CCA constitutes a measure for the study of environmental gradients and for the analysis of habitable spaces (Oksanen et al. 2019). Habitable space, in the sense given by Hutchinson (1957), is defined as a hypervolume composed of "n" dimensions, where each dimension represents one of the variables that allow the existence of a species (Pulliam 2000; Begon et al. 2006; Boulangeat et al. 2012); these variables are called resources, among which are food, substrates, climatic regimes, etc. (Colwell and Futuyma 1971). Furthermore, this concept of habitable space is widely related to the distribution of species (Pulliam 2000; Begon et al. 2006). Therefore, based on the above, the analysis carried out in this research can be considered an ecological niche analysis.

Leibold (1995) indicates the possibility of separating two different scenarios under which the ecological niche can be analyzed. In the first instance, the species occurs in all places where conditions are favorable, which is called the fundamental niche (Grinnell 1917); however, in reality, the species occupy only a part of this fundamental niche, presenting interactions with other species, and therefore they will be absent in those sites where there is a dominant competitor, which is known as the realized niche (Hutchinson 1957). Assuming that all butterfly species present biological interactions among themselves and with other species (Stork 2007; Lewinsohn and Roslin 2008; Maya-Martínez et al. 2009; Bonebrake et al. 2010) and taking into account that there was also significant global variation in the use of resources by the species (CCA, $p < 0.05$), then it can be established that: (1) the Sierra Chiquita and all its environmental conditions constitute the fundamental niche for all registered butterfly species; and (2) each of the evaluation units in which a species with a significant association by the variables was observed represented a fraction of its realized niche. The above acquires great relevance, taking into account that the butterfly community had never been analyzed from the ecological niche approach; this allows the species to be used as indicators of the ecological quality of an ecosystem, in this case,

the plant communities evaluated from an elevational gradient, by comparing the niches of each of the species and the degree of connection between them.

In relation to the above, it has been pointed out that the presence of a species in a site is due to three limitations (Soberon and Peterson 2005): (1) the local environment, or the environmental variables that allow the population to grow; (2) the interactions with other local species (predation, competition, and mutualism) that allow the species to persist; and (3) site accessibility based on the species' dispersal abilities. Together, these three factors delimit the distribution of a species, and with them, the niche of the species can be reconstructed, considering the variables that exist in the site it occupies (Hirzel and Le Lay 2008). However, in practice, it is impossible to measure and analyze all the variables that can occur in natural conditions and that determine the niche of a species (Boulangeat et al. 2012).

Therefore, in this study only ten environmental variables were considered that were measured at the microhabitat level and that correspond to the previously mentioned niche approach, the most important being HI, DP, SR, CLA, and FP. Grinnell (1917) points out that the main local factors in the distribution of species are vegetation, food, shelter-mating sites, interspecific effects, and individual preferences, although perhaps the most important are climatic variables, including temperature (Guisan and Zimmermann 2000), since it has a direct effect on the behavior and physiology of organisms. In phytophagous insects, including butterflies, distribution is usually associated with vegetation, topography, altitude, climate, habitat, and human influence (DeVries and Walla 2001; Freitas et al. 2001; Ehrlich and Hanski 2004; Molleman et al. 2006; Schultz and Crone 2008; Schweiger et al. 2008; Uehara-Prado and Freitas 2009). In this study, temperature was not related to the distribution of the species. On the other hand, the heat index and dew point were significant variables that combine temperature and humidity. Then it can be pointed out that the union of both factors is of greater importance for the butterfly species in the study area. On the other hand, variables related to host plants were not analyzed, but their influence on butterflies has been widely studied (Scott 1986; De la Maza 1987; Luis and Llorente 1990; Vargas et al. 1994). It is likely that the dew point directly influences the plants, and in this way butterfly species respond indirectly to the presence of these plants, either using them as food or shelter (Hirzel and Le Lay 2008).

Conclusions

For the first time in north-eastern Mexico, butterflies were systematically sampled to monitor the plant communities along an elevation gradient of a Priority Region for Conservation of Biodiversity. A total of 38,011 specimens belonging to six families, 20 subfamilies, 38 tribes, 129 genera, and 195 species of butterfly were collected from the study area. The highest abundance and richness of species, as well as alpha diversity, were recorded in the lowest elevation sites and decreased significantly with increasing altitude. The tendency of altitudinal distribution of the Papilionoidea butterflies in Sierra Chiquita is well defined to the environmental characteristics of the lower zone, agreeing with the Rapoport rule. The sites of low and intermediate altitude constitute an area of distribution of tropical species, while the site of the third floor forms an independent group of high mountain species.

The seasonality effect was absent on species richness; however, for species abundance, the differences between dry season and rainy season were significant in each site, except for the comparison between sites with TF and GF vegetation. The geographical location of the study area plus the different plant compositions of the sampled sites could be the main reason for the variation found here in the butterfly communities with altitude and season. In addition, relative humidity and temperature can influence the community of Papilionoidea in the study area; however, both abiotic factors directly affect plant composition, which is assumed to be the main factor in determining the composition and abundance of butterfly species.

The association between environmental variables and the community of Papilionoidea along the elevational gradient was significant, with the conditions of HI, DP, SR, CLA, and FP being the variables that best describe the species composition in the Sierra Chiquita. The information presented here provides reference data that allow the comparison of the diversity and richness of Papilionoidea species at a regional and national scale. This information could be used as an initial step to analyze the possible use of butterflies as a biodiversity indicator group in Mexico.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Author contributions

EMJ sampling sites selection, fieldwork, butterflies identification, data analysis and document writing; LSC fieldwork, database compilation and document writing; JMCB butterflies identification, database compilation and document writing; MTJSM butterflies identification and completed document review; CMCA data analysis, results interpretation and completed document review.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Sampling data by vegetation type in the Sierra Chiquita, Mexico

Authors: Edmar Meléndez-Jaramillo, Laura Sánchez-Castillo, Juana María Coronado-Blanco, Ma. Teresa de Jesús Segura-Martínez, César Martín Cantú-Ayala

Data type: docx

Explanation note: Coordinates at plot center; elevation in meters.

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Link: https://doi.org/10.3897/neotropical.19.e136190.suppl1

Supplementary material 2

Taxonomic list and abundance of species found by vegetation community in the Sierra Chiquita

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Data type: docx

Explanation note: Legend: TF = Thorn forest, TTS = Tamaulipan thornscrub, SS = Submountain scrub, GF = Gallery forest, OF = Oak forest, OPF = Oak and pine forest, CF = Cloud forest. The marked species (*) are significant ($p < 0.05$) according to the Monte Carlo permutation test.

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